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Stem chondrichthyan microfossils from the Lower Old Red Sandstone of the Welsh Borderland

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ABSTRACT:

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Placoid and polyodontode scales of stem chondrichthyans have been found in the early Lochkovian "Ditton Group" of the Brown Clee Hill district, Shropshire, England and at Talgarth, south Wales. One of the forms is assigned to a new species of *Altholepis* Karatajūtė-Talimaa, 1997, a genus already recognised from Lochkovian shallow marine deposits in Celtiberia, Spain and the Northwest Territories, Canada as well as the type locality in Podolia, Ukraine. *Altholepis salopensis* sp. nov. is based on small polyodontode scales with typically three to eight high odontodes; the scale form was previously considered to belong to acanthodian "*Nostolepis*" *robusta* (Brotzen, 1934). The structure of other scales formerly assigned to "*Nostolepis*" *robusta* has led us to erect a new genus *Jolepis* for this scale form, which differs from *Altholepis* in lacking an ordered layout of odontodes. *Jolepis robusta* (Brotzen, 1934), originally (and possibly still) considered to be an acanthodian, is also known from the Baltic countries, Russia, and northern Germany (ex erratic limestones). Scales of acanthodian *Parexus recurvus* Agassiz, 1845, and/or possibly from the stem chondrichthyan *Seretolepis elegans* Karatajūtė-Talimaa, 1968 (scales of these two taxa are barely distinguishable), and of stem chondrichthyan *Polymerolepis whitei* Karatajūtė-Talimaa, 1968 are also present. *Altholepis*, *Jolepis* gen. nov., *Seretolepis* Karatajūtė-Talimaa, 1968 and *Polymerolepis* Karatajūtė-Talimaa, 1968 are found in marine deposits elsewhere; the British occurrence of these taxa adds to the debate on the sedimentological origins of the Lower Old Red Sandstone deposits in the Welsh Borderland. The geographic range of several early sharks is now known to extend around the Old Red Sandstone continent and beyond.

Keywords: Scale histology; Palaeobiogeography; Lower Devonian (Lochkovian), Stem gnathostomes; Altholepis; Polymerolepis; British Isles.

INTRODUCTION

Microfossils of thelodonts, heterostracans, cephalaspids, anaspids and various gnathostomes (sometimes designated "ichthyoliths", hereafter "microvertebrates") are common throughout the upper Silurian to Lower Devonian (Lower Old Red Sandstone; LORS) in the Welsh Borderland (generally Worcestershire, Shropshire, Herefordshire, Gloucestershire, and eastern Welsh counties). They have been known for over 180 years, but only in recent decades have the rarer elements been recognised (Turner *et al.* 2014, 2017a, b). Turner (1984) found one scale in a Brown Clee sample (Dairy Dingle), which has since been recognised as the chondrichthyan described below as *Altholepis* Karatajūtė-Talimaa, 1997; she passed on such non-thelodont material to J.M.J. Vergoossen, who was thus the first to illustrate possible chondrichthyan scales, which he assigned to "*Nostolepis*" *robusta* (Brotzen, 1934), *Polymerolepis whitei* Karatajūtė-Talimaa, 1968, cf. *Polymerolepis*, and Cladodontida? sp. 1 (Vergoossen 1999).

Characters traditionally used to distinguish between acanthodian and (growing) chondrichthyan scales include the type of growth of the crown, with the former showing periodic addition of concentric growth zones (Denison 1979); some chondrichthyan scales show concentric addition of base bone lamellae, with or without cell lacunae (e.g., *Cladodus gunnelli* Wells, 1944; *Protacrodus wellsi* Gross, 1973), but not of crown growth zones (Karatajūtė-Talimaa 1998). However, identification of isolated scales as either chondrichthyan or acanthodian has been blurred in recent years, with the recognition of acanthodians as stem chondrichthyans (e.g., Zhu *et al.* 2013; Burrow *et al.* 2016), and the description of chondrichthyan-type areal and apposed growth scales in climatiid acanthodians (Burrow *et al.* 2013, 2015).

Here we describe newly recognised Lochkovian chondrichthyan scales collected in recent years from several localities within the classic Brown Clee Hill outcrop and southern Wales (e.g., Ball and Dineley 1961; Turner 1973a, b; Turner *et al.* 2017a).

MATERIAL AND METHODS

Standard acid digestion methods, using acetic acid, were employed to breakdown calcareous rocks, with "Kilrock" or microwave oven employed for more quartzitic samples. Scales were imaged uncoated, using an Hitachi Tabletop TM-1000 environmental scanning electron microscope (ESEM) at the Queensland Museum, Brisbane, Australia; a few scales were photographed using a light microscope and camera. Scale sections were ground manually using 1200- and 2000-grit wet and dry sandpaper, fixed to glass slides with Crystalbond-30, covered with Eukitt mounting medium and a coverslip, and imaged using an Olympus BX-50 microscope and DP-12 imaging system. Drawings were done manually by CJB and figures compiled using Photoshop CS4 by CJB.

Institutional abbreviations: BGS MPK, British Geological Survey; NHMUK PV P, Natural History Museum (London) vertebrate palaeontology; NMW, National Museum of Wales; SHRMS, Shropshire Museums (Ludlow).

SYSTEMATIC PALAEONTOLOGY

Chondrichthyes Huxley, 1880
Order Altholepidiformes Andreev, Coates, Shelton, Cooper, Smith and Sansom, 2015

REVISED DIAGNOSIS: Fish with growing polyodontocomplex scale crowns developed through sequential addition of component odontodes in posterior and lateral directions. Primordial scale odontode the largest. Odontode length varies within odontocomplexes.

REMARKS. Andreev *et al.* (2015) identified the primordial odontode as the most anterior; however, this is not the case in *Altholepis salopensis* sp. nov., and therefore we have omitted this character in revising their diagnosis.

Family Altholepididae Andreev, Coates, Shelton, Cooper, Smith and Sansom, 2015
Genus *Altholepis* Karatajūtė-Talimaa, 1997

TYPE SPECIES: *Altholepis composita* Karatajūtė-Talimaa, 1997.

REVISED DIAGNOSIS (after Karatajūtė-Talimaa 1997 and Martínez-Pérez *et al.* 2010): Small subrhombic to oval scales up to 1.5 mm wide and 1.0 mm long; crown formed of multiple wedge-shaped odontodes, with primordial odontode surrounded by one or more odontodes on each side and posteriorly; all odontodes subparallel and oriented anteroposteriorly; odontodes with transversely concave upper surface and pointed posterior end; basal surface of scale flat or slightly concave, and pierced by numerous canal openings, with sharp rim between basal surface and sloping neck; pulp canals run longitudinally through each odontode; outer layer of odontode filled with fine branching dentine tubules running into thick dentine network surrounding pulp canals.

REMARKS: Based on partial articulated specimens of *Altholepis* spp. from the Lochkovian Man on the Hill (MOTH) locality in the Northwest Territories, Canada, Hanke (2001) considered that only the holotype and one other scale figured by Karatajūtė-Talimaa (1997, pl. 1P, T) are from *A. composita*, whereas the other scales might be assignable to a different species; one of those scales (Karatajūtė-Talimaa 1997, pl. 1U) is most like the scales that Martínez-Pérez *et al.* (2010) assigned to *A. composita* and which too might belong to another species. Hanke (2001) also thought that the three (as yet unpublished) *Altholepis* spp. that he recognised from the MOTH locality differ from each other in fin spine, as well as scale, morphology. He also noted that, contra the original description of *A. composita* by Karatajūtė-Talimaa (1997, fig. 4A), scales of all three putative species (including *A. composita*) found at MOTH likely had bone cell lacunae in the base. Furthermore, Hanke (2001) described all his three MOTH species as having oriented mesodentine (= Stranggewebe *sensu* Gross 1971) in the crown odontodes (Hanke 2001, figs 36.1–4, 38, 42.2).

Altholepis salopensis sp. nov.
(Text-figs 1A–O, 2A, B)

part 1995. "*Nostolepis*" *robusta*; S. Turner, J. Vergoossen and R. Williams, pp. 377, 379.
part 1999. "*Nostolepis*" *robusta*; J. Vergoossen, pp. 41, 60, tables 1, 2, figs 21–23 [non fig. 19 = *Jolepis robusta* (Brotzen, 1934)].
part 2000. "*Nostolepis*" *robusta*; J. Vergoossen, p. 188, table 1.
part 2017a. *Altholepis* sp.; S. Turner, C. Burrow, P. Tarrant and R. Williams, pp. 460, 475, tables 2, 3.
2017a. *Altholepis* sp.; S. Turner, C. Burrow, P. Tarrant and R. Williams, figs 8O, P.

ETYMOLOGY: Latin, from Shropshire in the Welsh Borderland, for the origin of the type and most of the material described here.

HOLOTYPE: NHMUK PV P.67625 from Hudwick Dingle 4, Brown Clee, Shropshire (SO 6329.9224). Zoobank ID: urn:lsid:zoobank.org:pub:5539019A-AD9A-4602-AAAD-92F5E14AC589.

OTHER MATERIAL EXAMINED: Paratypes: eleven scales including NHMUK PV P.67622–4, 67626–8 (another scale NHMUK PV P.67621 was lost in transit: this scale was incorrectly captioned in Turner *et al*. (2017a, fig. 8P) as BGS MPK 14592, which is the scale in their figure 8O that is captioned as NHMUK PV P.67621(2)), and scale thin sections NHMUK PV P.67633, 67634 from Hudwick Dingle 4. Also four scales including NHMUK PV P.67630 and one scale thin section NHMUK PV P.67632 from Bouldon Ford (SO 5496.8499), two scales BGS MPK 14592 and BGS MPK 14643 from Lower Hayton (SO 5056.8098), scales including NHMUK PV P.67631 from Besom Farm (SO 6076.8094), two scales (Vergoossen 1999, fig. 23) from Dairy Dingle 2, one scale SHRMS: 2017.00039 from Dog Ditch Dingle (SO 5470.8059), all Shropshire; at least 12 scales from Cwm Trappy (SN 6501.2105), one scale from Talgarth site 4 (SO 1695.3258), Pwll-Y-Wrach section, Powys, south Wales (All Welsh scales are NMW).

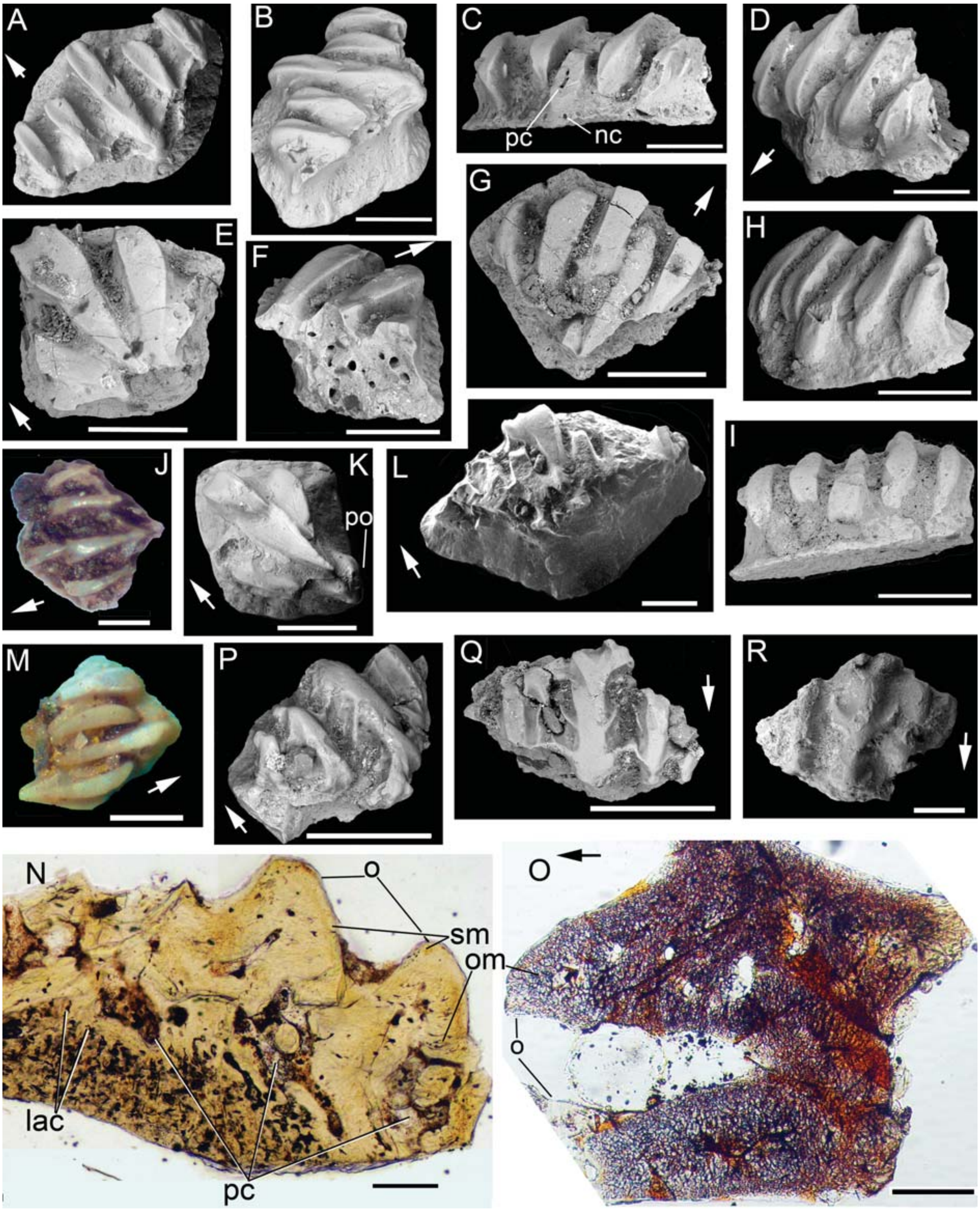
DIAGNOSIS: Small scales less than 1.5 mm long, wide and high, with as few as three and up to eight high ridged odontodes generally angled to the posterior point and having new odontodes added anteriorly as well as posteriorly and laterally; weak or no side ridges on odontodes, which are separated from odontodes beside them by a space as wide or wider than the width of the odontodes; base larger than crown with diamond or subrhombic base outline; rare canal openings low on neck; wide pulp canal running longitudinally through base of each odontode; syncitial mesodentine in outer region of odontodes, odontocytic mesodentine and cell lacunae in base of odontodes; possible cell lacunae in lamellar bone base.

DESCRIPTION: Scales are up to 1.0 mm long, 1.3 mm wide and less than 1.0 mm high with a diamond or subrhombic shape in dorsal/ventral view (Text-figs 1A–M, 2A, B). The crown comprises three (e.g., Text-fig. 1E) or more (up to eight in some, e.g., Text-fig. 1L, M) anteroposteriorly subparallel elongate odontodes, quite widely separated laterally from each other; width of grooves is equal to or wider than the ridges.

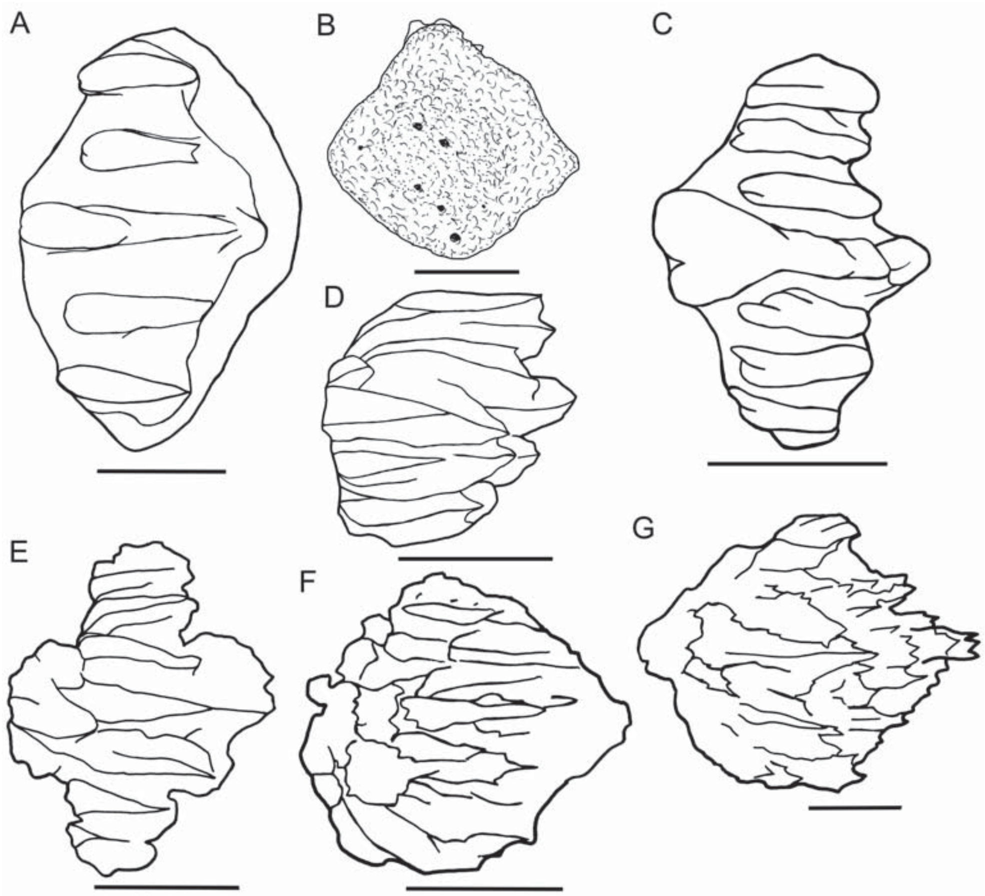
Based on the range of scales observed, the general pattern of growth is regulated, with the central odontode formed first, followed by an anterior odontode that overlaps the primary one, and two odontodes laterally (Text-fig. 1E, K). Another odontode was then added to each side, with more odontodes added anterior and posterior to the existing odontodes as well as laterally (Text-fig. 1M). Short odontodes on the posterior corner of the scale form a separate crown area (Text-fig. 1G, J, K, M). On most scales, the central odontode is the longest, but on rare scales the central odontode is short (Text-fig. 1I). The odontode upper surfaces are mostly transversely concave, and they terminate posteriorly at a sharp point. Ridges are ornamented in some scales laterally by faint angled grooves, which may have been obscured by wear to the scales. In most *A. salopensis* sp. nov. scales the odontodes rise up towards the posterior so that the scale increases in height posteriad (Text-fig. 1B, F).

The scale base is flat or slightly concave, and multiple canal openings, c. 0.02 mm diameter, are visible on the basal surface which is rough, with a fine scalloped or reticulated patterning (Text-fig. 2B). Some canals open out low on the neck (Text-fig. 1B, C, D, E).

Histological section transversely across a scale (Text-fig. 1N) shows a wide pulp canal running longitudinally at the base of each odontode, with fine syncitial mesodentine (*sensu* Valiukevičius and Burrow 2005, mesodentine lacking lacunal widenings) in the upper area of the odontodes transitioning



Text-fig. 1. Scales of *Altholepis* spp. from the Welsh Borderland. **A-O** – *Altholepis salopensis* sp. nov. A-G, P-Q – specimens from Hudwick Dingle 4 [original sample NHMUK PV P.52611]: A, B – scale NHMUK PV P.67621 previously figured (Turner *et al*. 2017, fig. 8P), now lost, crown and laterocrown views; C, D – holotype NHMUK PV P.67625, anterior and oblique views; E – paratype NHMUK PV P.67626, crown view; F – paratype NHMUK PV P.67627, posterior view; G – paratype NHMUK PV.P.67628, crown view. H, I – BGS MPK 14592, antero-dorsal and anterior views, and J – BGS MPK 14643, crown view, from Lower Hayton (sample JD841); K – SHRMS: 2017.00039 from Dog Ditch Dingle, crown view; L – NHMUK PV P.67630 from Bouldon Ford; M – NHMUK PV P.67631 from Besom Farm sample NHMUK PV P.52631, crown view; N, O – thin sections of scales: N – vertical transverse section NHMUK PV P.67632 from Bouldon Ford; O – horizontal →



Text-fig. 2. *Altholepis* spp. scale comparative outline drawings. **A**, **B** – *A. salopensis* sp. nov. of Welsh Borderland: A – NHMUK PV P.67621, (lost) scale in Text-fig. 1A; B – SHRMS: 2017.00039, basal view. **C** – *A. composita* Karatajūtė-Talimaa, 1997 of Podolia; holotype (after Karatajūtė-Talimaa 1997, pl. 1P). **D** – *A. "composita"* Karatajūtė-Talimaa, 1997 of Spain (after Martínez-Pérez *et al*. 2010, fig. 3A). **E** – *A. composita* Karatajūtė-Talimaa, 1997 of Northwest Territories, Canada (Hanke 2001, fig. 35.5). **F** – *A.* sp. 1 of Northwest Territories, Canada (after Hanke 2001, fig. 37.11). **G** – *A.* sp. 2 of Northwest Territories, Canada (Hanke 2001, fig. 41.8) (Drawings by CB). Scale bar = 0.3 mm

to a network of thick odontocytic mesodentine (*sensu* Valiukevičius and Burrow 2005, mesodentine with lacunal widenings) through the rest of the crown; the latter is best seen in the horizontal section through the lower crown (Text-fig. 1O). Dentinous odontodes formed on top of the lamellar bone base. The base appears to be filled with large stellate lacunae, but regulated position of these structures at the junction of basal bone lamellae parallel to the base and Sharpey's fibres radiating through the base could indicate that these structures are taphonomic artefacts; however, there does appear to be a transition from these to proper mesodentine in the base of the crown indicating that at least some of them are bone cell lacunae (Text-fig. 1N, lac).

COMPARISON: In general *A. salopensis* sp. nov. scales have fewer and wider separated odontodes and a comparatively larger base than *A. composita* from the Chortkov Regional Stage (Lochkovian) Podolia (Text-fig. 2C). The original description by Karatajūtė-Talimaa (1997) of scales of the type species *A. composita* also gave no mention of new odontodes added anteriorly, unlike the scales of *A. salopensis* sp. nov. *Altholepis composita* was also described as having well-developed side ridges branching off the odon-

section through crown NHMUK PV P.67626 from Hudwick Dingle 4; **P-R** – *Altholepis* sp. aff. *A. composita* Karatajūtė-Talimaa, 1997. P, Q – scale NHMUK PV P.67629 from Hudwick Dingle 4, laterocrown and crown views; R – scale NMW.2017.13G.11 from Cwm Trappy, crown view. A-I, K-M, P-R – ESEM images; J, M – light microscope images. lac, lacunae; o, odontodes; om, odontocytic mesodentine; pc, pulp canal; po, posterior crown odontodes; sm, syncitial mesodentine. Arrows indicate anterior direction. Scale bar = 0.3 mm in A-M, P-R, 0.1 mm in N, O todes, orthodentine forming the odontodes, and an acellular bone base. The type *A. composita* scales have crowns that obscure the base, whereas the basal rim always extends beyond the crowns in *A. salopensis* sp. nov. The only scales in the British material similar to the types of *A. composita* are the three scales that we assign to *A.* sp. aff. *composita*, below.

Based on comparison with the squamation on articulated MOTH *Altholepis* specimens, Hanke (2001) observed that only the holotype and one other type scale of *A. composita* figured by Karatajūtė-Talimaa (1997, pl. 1P, T) conformed to the scale forms seen on the articulated MOTH fish that he assigned to *A. composita* (Text-fig. 2E), with the other scales corresponding to forms on one of his other two purported species (*A.* nov. sp. 1, 2; Text-fig. 2F, G). Scales of the slightly older *A. salopensis* sp. nov. closely resemble those of *A. composita*, differing in having few or no side ridges on the odontodes, wide grooves between the odontodes and possibly lateral fine grooves on the odontodes, and in the histological structure. Scales from the Lower Devonian (Lochkovian) of Spain which Martínez-Pérez *et al.* (2010) referred to *A. composita* (Text-fig. 2D) differ from those of *A. salopensis* sp. nov. and most of the type *A. composita* in having broad overlapping flanges on the odontodes, indicating they could also be from a different species.

As mentioned above, Hanke (2001) noted in his description of the much more abundant scales and partial articulated specimens of *Altholepis* spp. from MOTH that the scale crowns are mostly filled with "oriented mesodentine", commonly referred to as Stranggewebe (*sensu* Gross 1971), a tissue that extends between vascular canals in climatiid and "nostolepid" acanthodians. However, based on histological drawings of the MOTH scales (Hanke 2001, figs 36.1–4, 38, 42.2), the tissue appears rather to be Spiralfasern *sensu* Gross (1973), a structure that has been observed around the pulp canals in isolated putative chondrichthyan scales (e.g., Gross 1973, fig. 18) as well as in scales of an articulated chondrichthyan *Gogoselachus lynbeazleyae* Long, Burrow, Ginter, Maisey, Trinajstic, Coates, Young and Senden, 2015 (Long *et al.* 2015, fig. 7N, O), where the tissue was recognised as a spiral infilling of the pulp canal. With the limited material of *A. salopensis* sp. nov. available to us, we only sacrificed a few scales for sectioning, none of which show evidence of Stranggewebe or Spiralfasern in the crown.

Some of the scales from the "Dittonian" (Lochkovian) erratics of northern Germany, which Gross (1971, pl. 6, figs 12, 16, 17) assigned to *Nostolepis robusta*, conform to the morphotype of *Altholepis* scales. Gross (1971) noted that the regular arrangement of the ridges into transverse rows resembled that in scales of the 'cladoselachian' *Ohiolepis* Wells, 1944 from the Middle Devonian of North America. Scales from the upper Lower Devonian (Emsian) of southeastern Australia (Giffin 1980; Burrow 1997, pl. 5.16), the Emsian Xiejiawan Formation, Longmenshan, China (Burrow *et al.* 2000), and Germany (Friman 1983; Poltnig 1984) have also been assigned to *Ohiolepis*. However, scales of the type species *Ohiolepis newberryi* Wells, 1944 from the Ohio bonebed type localities differ from those of *Altholepis* in not having side ribs on the odontodes or a separate posterior crown area, with odontodes being laterally contiguous with each other, and having a convex base lacking canals. Despite being younger than most other records of *Altholepis*, some of the scales from China (Burrow *et al.* 2000, pl. 10 figs. 8, 12) do resemble those of *Altholepis* rather than *Ohiolepis*, in having separate subparallel odontodes and canal openings piercing the base.

STRATIGRAPHIC AND GEOGRAPHICAL DISTRIBUTION: Ditton Group = Freshwater West Formation of Barclay *et al.* (2015) = "PL Group" *sensu* Vergoossen 1999 (lower–mid Lochkovian), Welsh Borderland, southern Britain: Shropshire: Aston Hill, Besom Farm, Bouldon Ford, Clapgate Cottages, Dairy Dingle, Dog Ditch Dingle, Hudwick Dingle 4, Little Oxenbold, Lower Hayton, Stock Hall 4, Sudford Dingle; Wales: Cwm Trappy and Pwll-Y-Wrach Site 4, near Talgarth (see Turner *et al.* 2017a, app. 2 for locality details).

Altholepis sp. aff. *A. composita* Karatajūtė-Talimaa, 1997
(Text-fig. 1P–R)

MATERIAL EXAMINED: One scale NHMUK PV P.67620 and scale thin section NHMUK PV P.67629 from Hudwick Dingle 4, and scales from Bouldon Ford, Shropshire; two scales NMW 2017.13G.11, 12 from Cwm Trappy, Wales.

DESCRIPTION: These scales (Text-fig. 1P–R) differ from those of *A. salopensis* sp. nov. in having robust subparallel ridges with strong side ridges branching off and crossing the inter-ridge trough. They lack a clear margin around the perimeter of the scale, although the Cwm Trappy scales are strongly abraded, obscuring fine details.

COMPARISON: These scales resemble some of the type material of *A. composita* (cf. Karatajūtė-Talimaa 1997, pl. 1, figs R, S) in showing strong side ridges branching off the odontodes. Hanke (2001) considered those *A. composita* scales to belong to one of the other purported MOTH *Altholepis* species (Text-fig. 2G). Scales of the latter, however, differ from the Welsh Borderland scales in having sharp crests and serrated ridges, although this difference could be caused by abrasion of the Welsh Borderland scales. Given the paucity and poor preservation of the material, for now we tentatively refer the latter scales to *A.* sp. aff. *A. composita*.

Order Polymerolepidiformes Karatajūtė-Talimaa, 1968
Family Polymerolepididae Karatajūtė-Talimaa, 1968
Genus *Polymerolepis* Karatajūtė-Talimaa, 1968

TYPE SPECIES: *Polymerolepis whitei* Karatajūtė-Talimaa, 1968.

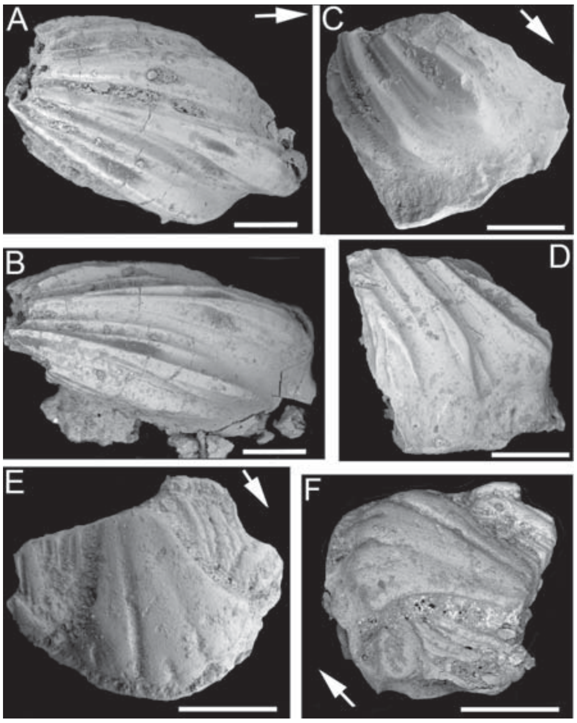
Polymerolepis whitei Karatajūtė-Talimaa, 1968
(Text-fig. 3)

MATERIAL EXAMINED: Two scales SHRMS: 2017.00040, 41 from Dog Ditch Dingle; one scale SHRMS: 2017.00042 from Little Oxenbold; and two scales from Netchwood Common (Vergoossen 1999, figs 25, 26).

DESCRIPTION: The scales are extremely rare in the LORS, with only six identified from the Welsh Borderland. Vergoossen (1999, figs 25, 26) assigned the two scales from Netchwood Common to *P. whitei* and cf. *Polymerolepis* respectively. Of the new material, only the main central crown and base of scale SHRMS: 2017.00040 (Text-fig. 3A, B) is preserved, and it has been abraded like many of the scales from the Ditton Group/Freshwater West Formation, but it still shows characteristic features of body scales of *Polymerolepis* (e.g., Karatajūtė-Talimaa 1998, fig. 6J, K), with multiple serrated ridges covering the high crown, a flat or concave base, and a vacuous internal structure (Text-fig. 3A, B). Scale SHRMS: 2017.00041 shows a similar structure (Text-fig. 3C, D). Scale SHRMS: 2017.00041 (Text-fig. 3E, F) from Little Oxenbold has a lower crown, with a wide higher triangular area anteromedially and close-set narrow serrated ridges extending anteroposteriorly on the lower side areas.

COMPARISON: The type material of *P. whitei* from Podolia shows a wide range of scale morphotypes (e.g., Obruchev and Karatajūtė-Talimaa 1967, pl. 2 figs 1–4; Karatajūtė-Talimaa 1998, figs. 6, 7), and Hanke *et al.* (2013, figs 1–5) demonstrated in their description of a partial articulated specimen from the MOTH locality, that the scale variation over the body is even greater than seen in the type scales. The Dog Ditch Dingle scale forms correspond most closely to the kind along the leading edge of fins (Hanke *et al.* 2013, fig. 4B, D), which have smoother ridges than the body scales. The Little Oxenbold scale crown matches one of the forms designated body scales by Karatajūtė-Talimaa (1977, fig. 3.15, 1998, fig. 6K_1). The Netchwood Common scale forms with complex crowns, comparable to one of the morphotypes in the type material (Karatajūtė-Talimaa 1977, pl. 3, fig. 19A), were not found on the partial articulated fish from MOTH, but the latter is just an anal fin and part of the caudal fin and peduncle so only preserves a limited area of squamation.

Specimens referred to *P. whitei* from the younger Windmill Limestone, Simpson Park Range, Nevada



Text-fig. 3. *Polymerolepis whitei* Karatajūtė-Talimaa, 1968 from the Welsh Borderland. A-D – from Dog Ditch Dingle. A, B – SHRMS: 2017.00040, broken scale in crown and lateral views; C, D – SHRMS: 2017.00041, crown and anterolateral views; E, F – SHRMS: 2017.00042 from Little Oxenbold, crown and laterocrown views. Arrow indicates anterior direction. Scale bar = 0.3 mm include head, fin and body scales (Turner and Murphy 1988, table 1, figs 2.14, 15, 20, 22–26).

STRATIGRAPHIC AND GEOGRAPHICAL DISTRIBUTION: All Lochkovian: Ditton Group = Freshwater West Formation of Barclay *et al.* (2015), Welsh Borderland, southern Britain: Brown Clee; Shropshire (Turner *et al.* 2017a): Dog Ditch Dingle, Hudwick Dingle 4, Little Oxenbold, Netchwood Common; Podolia, Ukraine: Chortkov Regional Stage; Canada: Delorme Formation, Northwest Territories; USA: Windmill Limestone, Nevada.

?Acanthodii Owen, 1846

REMARKS: The species *Diplacanthoides robustus* was assigned by Brotzen (1934) to the "Acanthodidii" (i.e., the Acanthodii), and retained in the group by Gross (1971). Vergoossen (1999, 2000) considered the species to be better classified as a chondrichthyan, based on the apposed growth zones forming the crown, but as noted above many of the scales that he labelled as "*Nostolepis*" *robusta* are from *Altholepis*.

It is now considered likely that all acanthodians are stem chondrichthyans, based on recent phylogenetic analyses (e.g., Zhu *et al.* 2013; Burrow *et al.* 2016). Morphological and histological studies of the squamation of several LORS acanthodians known from the Midland Valley of Scotland have shown that *Parexus* has apposed growth scales hardly distinguishable from those of the putative chondrichthyan *Seretolepis elegans* Karatajūtė-Talimaa, 1968 (Burrow *et al.* 2013), and *Climatius* Agassiz, 1845 has areal growth scales (Burrow *et al.* 2015), thus blurring a traditional distinction between acanthodians and sharks. Because *Jolepis* gen. nov. (see below) shows the same histological structures found in "nostolepid" acanthodians, as well as *Climatius* and *Euthacanthus* Powrie, 1864 (see Newman *et al.* 2014), with Stranggewebe rather than Spiralfasern in the posterior crown growth zones, we tentatively retain the species in the Acanthodii.

Order and Family indet.
Jolepis gen. nov.

ETYMOLOGY: In honour of Dr Jo M. J. Vergoossen, for his work on Silurian–Early Devonian microvertebrate faunas.

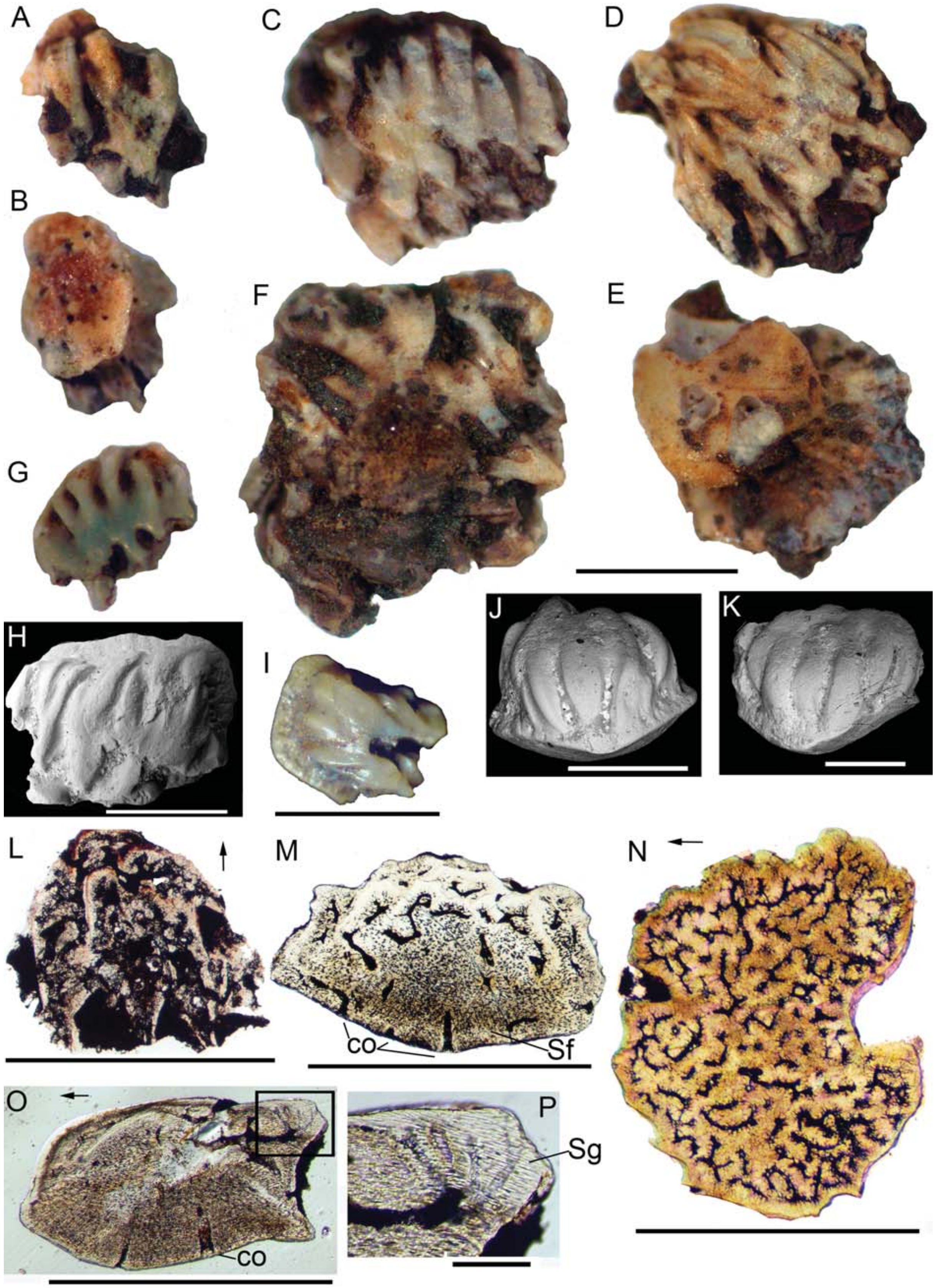
TYPE SPECIES: *Diplacanthoides robustus* Brotzen, 1934.

DIAGNOSIS: As for *Jolepis robusta* (Brotzen, 1934), type and only species. Zoobank ID: urn:lsid:zoobank.org:pub:CB1EC5DE-348A-41B1-8B51-56AF54 5250E2.

Jolepis robusta (Brotzen, 1934)
(Text-fig. 4)

1934. *Diplacanthoides robustus*; F. Brotzen p. 30, pl. 2, fig. 6a, b.
?1934. *Diplacanthoides hoppei*; F. Brotzen, p. 28, pl. 2, fig. 2a, b.
1934. *Diplacanthoides huckei*; F. Brotzen, p. 29, pl. 3, fig. 18a, b.
part 1947. *Nostolepis striata*; W. Gross, p. 134.
part 1971. *Nostolepis robusta*; W. Gross, p. 40, figs 15, 16, pl. 6, figs. 4−10 [non pl. 6, figs 12, 16, 17 = *Altholepis composita* Karatajūtė-Talimaa, 1997].
part 1979. *Nostolepis robusta*; R. Denison, p. 28.
?1980. *Nostolepis robusta*; J. Vieth, p. 9, figs 7, 14.
?1986. *Nostolepis robusta*; H. Mader, fig. 8.
part 1995. "*Nostolepis*" *robusta*; S. Turner, J. Vergoossen and R. Williams, pp. 377, 379.
part 1997. *Nostolepis robusta*; T. Märss, p. 28, figs 5, 8.
1997. *Nostolepis robusta*?; T. Märss, pl. 2, fig. 10.
1998. *Nostolepis robusta* (Brotzen); J. Valiukevičius, p. 31, pl. 5, figs 15–17, 19, pl. 6, figs 1, 2.
part 1999. "*Nostolepis*" *robusta*; J. Vergoossen, pp. 41, 58, 60, tables 1, 2, fig. 19 [non figs 21−23 = *Altholepis salopensis* sp. nov.].
part 1999. Cladodontida? sp. 1; J. Vergoossen, p. 72, fig. 28.
part 2000. "*Nostolepis*" *robusta*; J. Vergoossen, p. 188, table 1.

Text-fig. 4. *Jolepis robusta* (Brotzen, 1934) scales from the Welsh Borderland. A-H (light microscope images), L – scales from Cwm Trappy. → A, B – NMW.2017.13G.1, crown and base views; C – NMW.2017.13G.2, crown view; D, E – NMW.2017.13G.3, crown and base views; F – NMW.2017.13G.4, crown view; G – NMW.2017.13G.5, crown view; H – NMW.2017.13G.6, crown view (ESEM image); I – NHM PV P.67637 from Aston Hill sample NHM PV P.67517; J, K, O-P – scales from Scar Quarry, Dorstone, Herefordshire. J – NMW.2017.13G.8 (ESEM image); K – NMW.2017.13G.9 (ESEM image); O-P – NMW.2017.13G.10, vertical longitudinal section of scale, area boxed in O is shown magnified in P; L – NMW.2017.13G.7, horizontal section low in crown of scale; M, N – thin sections of scales from Little Oxenbold (Peter Tarrant sample SHRMS); M – vertical transverse section SHRMS: 2017.00043; N – horizontal section through base of crown SHRMS: 2017.00044. Anterior to upper left in A-G, I, to top in H, to bottom in J, K; images taken through light microscope unless indicated. co, canal openings; Sf, Sharpey's fibres; Sg, Stranggewebe. Scale bar = 1.0 mm in A-I, L-O, 0.5 mm in J, K, 0.1 mm in P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2000. *Nostolepis robusta*; J. Valiukevičius, p. 280, figs 1, 5, 6.
2005. *Nostolepis robusta*; J. Valiukevičius, pp. 361, 364, fig. 7, app. 4.
2017a. "*Nostolepis*" *robusta*; S. Turner, C. Burrow, P. Tarrant and R. Williams, pp. 474, 475, 476, 477, tables 2, 3, fig. 8K.

HOLOTYPE: Scale PMB f1191 (Brotzen 1934, pl. 2, fig. 6a, b; Gross 1971, pl. 6, fig. 7a, b: NB. Gross used Brotzen's material in his description) from Bey. 37, Lochkovian ("Dittonian") erratic limestone from the Beyrichienkalk, northern Germany; *Turinia pagei* Subzone (cf. Turner 1973a; Blieck and Elliott 2017).

MATERIAL EXAMINED: Forty scales including NMW.2017.13G.1–6 and thin section NMW. 2017.13G.7 from Cwm Trappy; six scales including NMW.2017.13G.8,9 and thin section NMW. 2017.13G.10 from Scar Quarry, Dorstone, Herefordshire (SO 308.434); ten scales from Talgarth site 5, Pwll-Y-Wrach (SO 1690.3270); four scales from Talgarth site 4, Pwll-Y-Wrach; six scales and two scale thin sections SHRMS: 2017.00043, 44 from Little Oxenbold (SO 5906.9177) (Peter Tarrant sample SHRMS), Shropshire.

DIAGNOSIS: Polyodontoid scales less than 3 mm wide with low crown formed of thick sinuous ridges; separate crown area in posterior half of scale; older crown growth zones only partially overlain by younger zones, which are added in an irregular pattern, with crown plus base growing circumferentially; flat or slightly convex base with ventral surface penetrated by multiple vascular canal openings; 3D-network of large calibre canals extending through the base and into the crown growth zones; Stranggewebe thickly developed in the posterior half, and mesodentine in the anterior half of the crown; gradual transition from base to crown with stellate bone cell lacunae through base and lower crown; Sharpey's fibres extending radially through base.

DESCRIPTION (adapted and revised from Gross 1971): The scales of *J. robusta* are relatively large compared with those of many other micromerically squamated stem gnathostome taxa, being up to 2.5 mm long and wide (Text-fig. 4F), and less than 1 mm high. The crown is relatively low and the sculpture ridges are quite broad and often curved or sinuous (Text-fig. 4D), of variable lengths and orientation, and usually with a rounded crest. The crown is subdivided into two regions, the larger extending back from the anterior edge, with the pointed posterior ends of the ridges overlapping the smaller posterior area, which bears shorter ridges that barely extend beyond the posterior limit of the base (Text-fig. 4C, D, H, I). The base has a subrhombic (Text-fig. 4I) or polygonal outline (Text-fig. 4B, E), is flat or slightly convex, and pierced by up to ten scattered vascular canal openings (Text-fig. 4B, E).

The histological structure (Text-fig. 4L–P) shows the irregular arrangement of partially superposed and apposed odontodes (Text-fig. 4L, M), an extensive network of vertical, horizontal and radial vascular canals throughout the base and crown (Text-fig. 4M–O; as the base grew the canals extended downwards maintaining the openings through the basal surface (Text-fig. 4M, O). Rarely, bone cell lacunae are arranged concentrically around the canals. Sharpey's fibres extend radially from the low apex of the base towards the basal surface (Text-fig. 4M, O). Stranggewebe is particularly well developed in the posterior half of the crown of many scales (Text-fig. 4P), and mesodentine more in the front half of the crown and in the ridges. Dentine tubules in the outer zone of the ridges are often sparse, forming a clear durodentine layer (Text-fig. 4M, O). In the front half of the crown the ridges are usually separate, but deeper layers show a partial overlapping of the growth zones (Text-fig. 4M).

COMPARISON: Gross (1971) noted that this scale type was found in the "Dittonian" erratics, but not in the older Silurian Beyrichienkalk. Co-occurring vertebrates included *Turinia pagei* Powrie, 1870, *Phialaspis* "*Traquairaspis*" *symondsi* (Lankester, 1868), *Corvaspis* Woodward, 1934, *Anglaspis* Jaekel, 1927 and several osteostracan genera, as well as acanthodians that he assigned to the genera *Nostolepis* Pander, 1856, *Gomphonchus* Gross, 1971 and *Poracanthodes* Brotzen, 1934, the same association that we find in the Welsh Borderlands (e.g., Turner *et al*. 2017a). Gross also observed that the scales were found in the Psammosteus Limestone of Britain, i.e., the basal Lochkovian. As well as scales that we recognise here as *J. robusta*, Gross (1971, pl. 6, figs 12, 16, 17) also included the forms with regularly laid out odontodes that we now recognise as *Altholepis*.

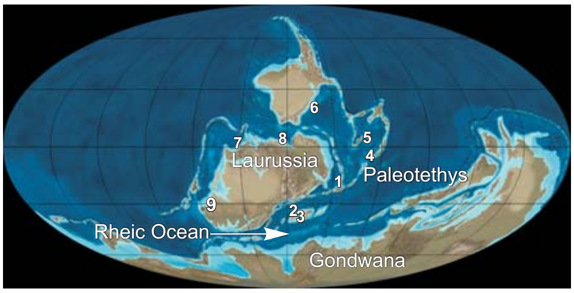
Vieth (1980, figs 7, 14) listed (but did not describe or figure) *N. robusta* from the upper Lochkovian Red Canyon River A, Ellesmere Island, arctic Canada, and Mader (1986, fig. 8) listed (but did not describe or figure) *N. robusta* from the lower Lochkovian of Palencia, Spain. Given that *Altholepis* was not erected until 1997, and *Altholepis* is now known to occur in both Spain and Canada, it seems possible that these older records might be *Altholepis* rather than *Jolepis* gen. nov. Clearly, the material needs to be re-examined.

Scales from the Luesma Formation (Lochkovian) of Zaragoza Province, Spain, which Mader (1986, fig. 17A, pl. 4, figs 1–5) assigned to a new genus and species *Iberolepis aragonensis* Mader, 1986 resemble those of *J. robusta* in crown view, but bases on *Iberolepis* scales are flat or concave, and their histological structure differs from that of *Jolepis* gen. nov. in lacking an extensive canal network and canal openings on the basal surface, in lacking bone cell lacunae, and in having Spiralfasern rather than Stranggewebe in the crown. Wang (1993, fig. 4, pl. 9, fig. 13) also recorded *Iberolepis* from the upper Lochkovian Nogueras Formation of Celtiberia, Spain. Scales of a younger taxon *Lunalepis leonensis* Mader, 1986 from the Pragian La Vid Formation, Leon and Nogueras Formation, Celtiberia, Spain also resemble those of *J. robusta*, but differ in being much smaller, having a high crown with a median longitudinal trough, and a base that is convex anteriorly and concave posteriorly (Mader 1986, pl. 4, figs 6–11). Although Mader (1986, pl. 4, fig. 11) recorded Stranggewebe in the posterior crown of *L. leonensis* scales, the tissue appears rather to be Spiralfasern.

STRATIGRAPHIC AND GEOGRAPHICAL DISTRIBUTION: Ditton Group = Freshwater West Formation of Barclay *et al.* (2015), lower–mid-Lochkovian, Welsh Borderland, southern Britain: Wales: Cwm Trappy, and Talgarth sites 4 and 5, Pwll-Y-Wrach, Powys; England–Herefordshire: Scar Quarry, Dorstone; Shropshire: Aston Hill, Besom Farm, Foxhole Coppice, Little Oxenbold (see Turner *et al.* 2017a, app. 2 for locality details); “Dittonian” erratics, north Germany (early Lochkovian); Jūra–Tilžė Regional Stages (upper Pridoli–Lochkovian), Baltic countries; Khatayakha Formation (lowermost Lochkovian), Timan-Pechora and Mikhailovsk Beds, Central Urals (lower Lochkovian), Russia; ?Red Canyon River A Formation, Ellesmere Island, arctic Canada (upper Lochkovian); ?Lebanza Formation, Palencia, Spain (?lower Lochkovian).

DISCUSSION

Vergoossen (1999) was the first to illustrate chondrichthyan remains from the Welsh Borderland, and our recent studies have brought to light new material of both polyodontode and placoid scales (Turner *et al.* 2017a, fig. 8Q) of stem chondrichthyans. Based on the



Text-fig. 5. Palaeogeographic reconstruction (after Blakey 2003, Mollweide projection map for the Early Devonian at http://cp-geosystems.com/400moll.jpg) showing localities known with late Pridoli and Lochkovian stem chondrichthyans around the Old Red Sandstone continent. 1, Welsh Borderland, UK; 2, Leon and Palencia, Spain; 3, Celtiberia, Spain; 4, Podolia; 5, Baltic countries; 6, central Urals, Russia; 7, Northwest Territories, Canada; 8, Arctic Canada archipelago; 9, Nevada, USA

new investigations into the microfossils from classic and new localities in Wales and the Welsh Borders, the chondrichthyans *Altholepis salopensis* sp. nov. and *A.* sp. aff. *A. composita* are newly added to the British faunal list, more rare material of *Polymerolepis whitei* has been identified, and the occurrence and morphotypes of the ?acanthodian/stem chondrichthyan *Jolepis robusta* from the Welsh Borderland have been clarified.

Fifty years ago, the first indications of faunal provinces around the Old Red Sandstone continent began to emerge (e.g., Halstead Tarlo 1967). Halstead and Turner (1973), Blieck (1984) and Dineley (1988), for instance, updated the concept based on the distribution of various LORS agnathans, and that work continues (e.g., Blieck and Elliott 2017; Turner *et al.* 2017a). Recent work shows that stem chondrichthyans are also widespread around the ORS continent (e.g., Dupret *et al.* 2011; Hanke *et al.* 2013; Turner *et al.* 2017a; Text-fig. 5). *Altholepis* and *Jolepis* gen. nov. are known from both marine and marginal marine deposits outside Britain – in Podolia (Ukraine), Spain, the Northwest Territories Canada and elsewhere. Scales of the acanthodian *Parexus recurvus* are hardly distinguishable from those of stem chondrichthyan *Seretolepis elegans*, with this scale form found in Podolia (Ukraine), Spain, Northwest Territories (Canada), and the Welsh Borderland. Similarly, the stem chondrichthyan *Polymerolepis* has been described from these same deposits, other than Spain. The presence of these widely distributed taxa adds to the debate on the sedimentological origins of the LORS deposits in the Welsh Borderland. These stem chondrichthyans might have entered freshwater settings (as most of the LORS is regarded to be by Barclay *et al.* 2015 based on their lithological data) or their presence with other far-ranging taxa such as thelodonts *Turinia* Traquair, 1896, *Nikolivia* Karatajūtė-Talimaa, 1978, etc., might suggest that not all the classic deposits are truly freshwater, as emphasised by Turner *et al.* (2017a).

Various palaeogeographic models have been put forward for the LORS timespan in recent years. Most of the taxa discussed here were probably limited to coastal shallow-water continental shelf environments rather than being capable of trans-oceanic migration. Thus we doubt the presence of a vast Rheic Ocean separating northern Gondwana and Laurussia by the late Pridoli to Lochkovian (see e.g., Turner *et al.* 2017a, fig. 10).

CONCLUSION

New fish microfossils of thelodonts, heterostracans, cephalaspids, anaspids and various gnathostomes found in the upper Silurian and Lower Devonian (Lower Old Red Sandstone: Ludlow–lower Emsian?) in the Welsh Borderland include the earliest known "shark" remains in Britain from the Lochkovian Ditton Group of the Welsh Borderlands (Brown Clee Hill Shropshire, Herefordshire) and Daugleddau Group near Talgarth, Powys in South Wales (Turner *et al.* 2017a, b).

The new taxon, *Altholepis salopensis* sp. nov., and other stem chondrichthyans described here extend the known range of several early sharks/gnathostomes around the Old Red Sandstone continent. These records increase our knowledge of the stratigraphic and geographic range of chondrichthyans in southern Britain and elsewhere in the early Devonian and especially for Wales.

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